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Zoogeography and composition of leech fauna of Danubian lowland rivers in the Kisalföld compared with some molluscs (Hirudinea, Gastropoda)

by
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Abstract: 24 species of Hirudinea were found in the alluvial floodplains of 7 rivers of the Kisalföld between 1987 and 1991. Ten of them are typical members of the Potamon biocoenosis and are restricted to the lowlands in the basin of the River Danube. The main distribution patterns are compared with those of some prosobranchiate snails (Thiaridae, Neritidae) and zoogeography is also concerned. A few Pontocaspian or Pontomediterranean species had not been recorded anywhere in Central Europe earlier.
Key words: Hirudinea, Gastropoda, distribution, lowland rivers

INTRODUCTION

Even today, the freshwater fauna of the River Danube is relatively unknown. The Pontocaspian rivers are the most important and oldest running waters in Europe. A permanent development of the European freshwater fauna has been taking place since Miocene drying up and dulcifying the former marine Paratethys Sea. The Preglacial Eumediterranean or Paleoeuropean fauna was formed using the former Egean river systems and the Pontosarmatian basins as a symmetry axis for spreading. Due to climatic changes during Pleistocene glaciation, the "oldest" groups (Thiaridae, Corbiculidae) have lost the northern part of their distribution and the fauna was influenced strongly by the more recent Eurosiberian fauna. The Danube became an important pathway to the northwest serving the invasion of formerly lost areas.

The most important characteristics of the recent faunal composition in the Central Pontocaspian and Sarmatian Basin were separation and relict character during the upper Pliocene and Pleistocene (BOTHÁR 1966, KROLOPP 1978, BALON 1968). While other parts of Europe were completely influenced by glaciation, here several species of the former fauna survived. At the same time the freshwater fauna of the listed basins developed further strongly.

In the light of geographical and faunal history the origin of the recent Danubian freshwater fauna is understandable. It comprises several groups with different distributional patterns: (a) Eurosiberian species with a wide distribution, (b) Pontocaspian and Pontosarmatian "endemic" species in the separated drainage area, e.g. *Limnomysis benedeni* (WEISH & TÜRKAY 1978) and (c) Pontomediterranean species. The faunal members of (b) and (c), which originated from the Paleoeuropean fauna (KINZELBACH 1987), have much more specifications and fossil connections to the Tertiary fauna. Therefore the Danube contains more freshwater species than other river basins. In this paper the first results of the study on faunal composition and species richness are presented for the freshwater leeches. Most of the species are similar regarding the main pattern of distribution. The biological classification of the investigated rivers is discussed. Zoogeographical barriers and pathways are also shown.

MATERIALS AND METHODS

From 1987 to 1991 the fauna of leeches, Prosobranchiate snails and Unionacean mussels was investigated in alluvial floodplains of the rivers in the Kisalföld. Qualitative samples were collected by hand from many localities and from different kinds of water bodies. The leeches were preserved in 70 % alcohol. The material has been given to the Hungarian Natural History Museum for documentation. Where no other data are presented, the specimens are from the author's collections.

RESULTS

The leech species found in seven rivers are listed in Table 1. The highest number was observed in the River Danube itself. Data of the partial biocoenosis were presented for the Austrian reaches, where fourteen species occur (NESEMANN 1989, 1990b). Downstream the Moson reach in Hungary the River Danube contains a leech fauna, which is completely different from that of the upper river. This is caused by the general change of environmental characteristics where the rivers leave the mountains and enter the plain. The morphology of the investigated rivers in the northwestern parts (Austrian Danube, Lajta) is strongly influenced by the mountains. Here the reaches are fast flowing and have strong bed load and gravelly or stony bottoms. In contrast the southeastern rivers (Hungarian Danube, March, Thaya, Rábca, Rába, Zala) have a low velocity of flow with loamy or sandy bottoms. The natural fall of the Danube changes at once from 40 cm per km to 7 cm per km downstream Gönyü. The main distribution patterns of many freshwater species are in accordance with these conditions.

Hirudinea

Fam. Glossiphoniidae

Glossiphonia paludosa (Caren , 1824) (Fig. 16)

Localities: Danube at Budapest (H), Szabadság-híd, km 1645.3, 15. Oct. 1988, leg. FORRÓ & NESEMANN; Ráckevei Duna near Szigethalom (H), 8. Jan. 1991, leg. FORRÓ & NESEMANN; Soroksári Duna near Dunaharaszti (H), 20. Jan. 1989, leg. FORRÓ & NESEMANN; Danube at Szalkszentmárton (H), km 1577.5, 31. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Dunaföldvár (H), km 1560.8, 31. Jan. 1991, leg. WIMMER & NESEMANN; Szentendre Duna between Tahitótfalu and Leányfalu (H), 7. Oct. 1989, leg. PUKY & NESEMANN; Danube at Vác (H), km 1680.4, 7. Oct. 1989, leg. PUKY & NESEMANN; Danube near Szob (H), km 1706.6, 7. Oct 1989, leg. PUKY & NESEMANN; Danube and Cuhai-Bakony-Ér near Gönyü (H), km 1789.8, 3. Apr. 1990; Danube downstream Gönyü (H), km 1783,1, Danube near Ásványráró (H), Dunaág, Felsősziget, km 1817, 23. Oct. 1990; Danube, oberer Tiergartenarm near Hainburg (A), 25. Apr. 1989; Danube near Mannswörth (A), in a dead-water reach, km 1917, 10. Feb. 1988; Danube-Kühwörther Wasser near Mühleiten (A), in a dead-water reach, Nov. 1990; Danube in the Lobau-area (A), Ölhafen, km 1920, Oct. 1990; Rába at Győr (H), 28. Jul. 1990; Lajta at Mosonmagyaróvár (H), 3. Apr. 1990; Leitha-Komitatskanal (Lajta bal parti csatorna) near Nickelsdorf

Table 1. List of leech species recorded in several lowland rivers of the Kisalföld until 1991.

	Duna	Morava	Lajta	Dyje	Zala	Rába	Rábca
Fam. **Piscicolidae** JOHNSTON 1865							
Cystobranchus respirans (TROSCHEL 1850)	O						
Cystobranchus fasciatus (KOLLAR 1842)	O			?			
Piscicola geometra (LINNAEUS 1761)	O	O	O	O	O	O	O
Piscicola haranti JARRY 1960							O
Fam. **Glossiphoniidae** VAILLANT 1890							
Glossiphonia complanata (LINNAEUS 1758)	O	O	O	O	O	O	
Glossiphonia verrucata (Fr. MÜLLER 1844)	O	O	O	O			
Glossiphonia paludosa (CARENA 1824)	O	O	O	O		O	
Glossiphonia concolor (APATHY 1888)	O	O	O		O		
Helobdella stagnalis (LINNAEUS 1758)	O	O	O	O	O	O	
Hemiclepsis marginata (O.F. MÜLLER 1774)	O	O	O	O	O		
Theromyzon tessulatum (O.F. MÜLLER 1774)	O	O	O	O	O	O	
Placobdella costata (Fr. MÜLLER 1846)	O						
Batracobdella algira (MOQUIN-TANDON 1846)	O						
Alboglossiphonia heteroclita (LINNAEUS 1758)	O	O	O	O	O	O	
Fam. **Hirudinidae** WHITMAN 1886							
Hirudo medicinalis LINNAEUS 1758	O	O	O	O	O		
Fam. **Haemopidae** SAWYER 1986							
Haemopis sanguisuga (LINNAEUS 1758)	O	O	O	O	O		
Fam. **Erpobdellidae** BLANCHARD 1894							
Erpobdella octoculata (LINNAEUS 1758)	O	O	O	O	O	O	O
Erpobdella nigricollis (BRANDES 1900)	O	O	O	O	O	O	O
Erpobdella vilnensis LISKIEWICZ 1925		O	O				
Erpobdella testacea (SAVIGNY 1822)	O	O			O		
Dina lineata (O.F. MÜLLER 1774)	O	O	O				
Dina punctata JOHANSSON 1927	O	O	O				
Dina apathyi GEDROYC 1916	O						
Trocheta cylindrica ÖRLEY 1886	O	O		O			
Total number of species	22	17	16	13	12	8	4

(A), Feb. 1989; March (Morava) near Markthof (A), 24. Mar. 1990; March near Stillfried (A), 29. Jul. 1990; March downstream Marchegg (A), 20. May 1990; March near Grub (A), 3. Jun. 1990; March at Marchegg (A), 20. May 1990; March, in a secondary branch near Schlosshof (A), from three samples, Feb. and Apr. 1990; March, in the main stream near Schlosshof (A), 22. Apr. 1990; March near Angern (A), 5. Aug. 1990; Thaya (Dyje), in a secondary branch near Rabensburg (A, CS), Aug. 1990.

The species is spread widely all over Central and Eastern Europe. It is common in some parts around the Mediterranean Sea. *G. paludosa* has a disjunct range of distribution in the northern and western parts of the settled area. Its occurrence is restricted only to some parts of plains and lowlands with a special warmer climate. The distribution has its centres in the Danube- and Po River basins (CHIAUDANI & MARCHETTI 1984). The species is a typical member of the Potamon biocoenosis. It is very common in the lower reaches of slow-flowing rivers of the Hungarian Great Plain, wherein it prefers gravel bottoms on sandy loam. *G. paludosa* has not occurred in the Danube upstream Vienna, it has not been found in the Upper Austrian and German reaches yet (NESEMANN 1991a). Its distribution in the Danube was proved to be very dissimilar by the author. In the upper reach of the settled area, where the conditions are similar to a torrential stream caused by strong gravity, *G. paludosa* is restricted to anabranches and dead-water reaches. Downstream the mouth of the River March, the nature of the Danube is gradually changing to a lowland river and the natural bed load is being reduced (Gönyü). Upstream until the Moson reach (Ásványráró), *G. paludosa* occurs frequently in the main stream and is present in high abundances throughout the whole Hungarian Danube.

Glossiphonia concolor (Apáthy, 1888) (Fig. 17)

Localities: Soroksári Duna near Dunaharaszti (H), Type-locality, 20. Jan. 1989, leg. FORRÓ & NESEMANN; Danube-Krumpenwasser near Stockerau (A), km 1948, 17. Mar. 1989; Danube-Lusthauswasser, a dead-water reach (Prater) near Vienna (A), 1988-1990; Danube, in a dead-water reach near Orth (A), 9. Oct. 1987; Danube-Kühwörther Wasser near Mühleiten (A), from several samples 1989-1990; Danube near Mannswörth (A), in a dead-water reach, 10. Feb. 1988; Zala SE Fenékpuszta (H), 20. Jun. 1990, leg. FORRÓ & NESEMANN; Zala in the Kis-Balaton reach (H), 21. Jun. 1990, leg. FORRÓ & NESEMANN; Lajta at Mosonmagyaróvár (H), 3. Apr. 1990; Leithakanal (Rét-árok) near Deutsch-Jahrndorf (A), May 1989; Leitha SW Pachfurth (A), dead-water reaches in the Auwinkel-area, 2. Jun. 1990, leg. MANN & NESEMANN; Leitha near Rohrau (A), in a secondary branch, 27. May 1990; Leitha near Pachfurth (A), Aug. 1990; Leitha between Seibersdorf and Bruck (A), from several localities, 1988-1990; March (Morava) N Grub (A), in a dead-water pond, 4. Jun. 1990; March near Schlosshof (A), in a dead-water reach, 22. Apr. 1990.

The complete range of distribution is not known, because *G. concolor* in former times was often confused with *Glossiphonia complanata* or considered under this name. According to LUKIN (1976), NESEMANN (1990a) and other authors, the species occurs in most parts of Europe with a concentration in the southern parts of the European part of the Soviet Union, the Danube Basin and some lowlands in the northern and eastern parts of Central Europe. The distribution patterns are generally very similar to that of *G. paludosa*, but the ecological preferences are quite different. *G. concolor* occurs in large numbers in old bran-

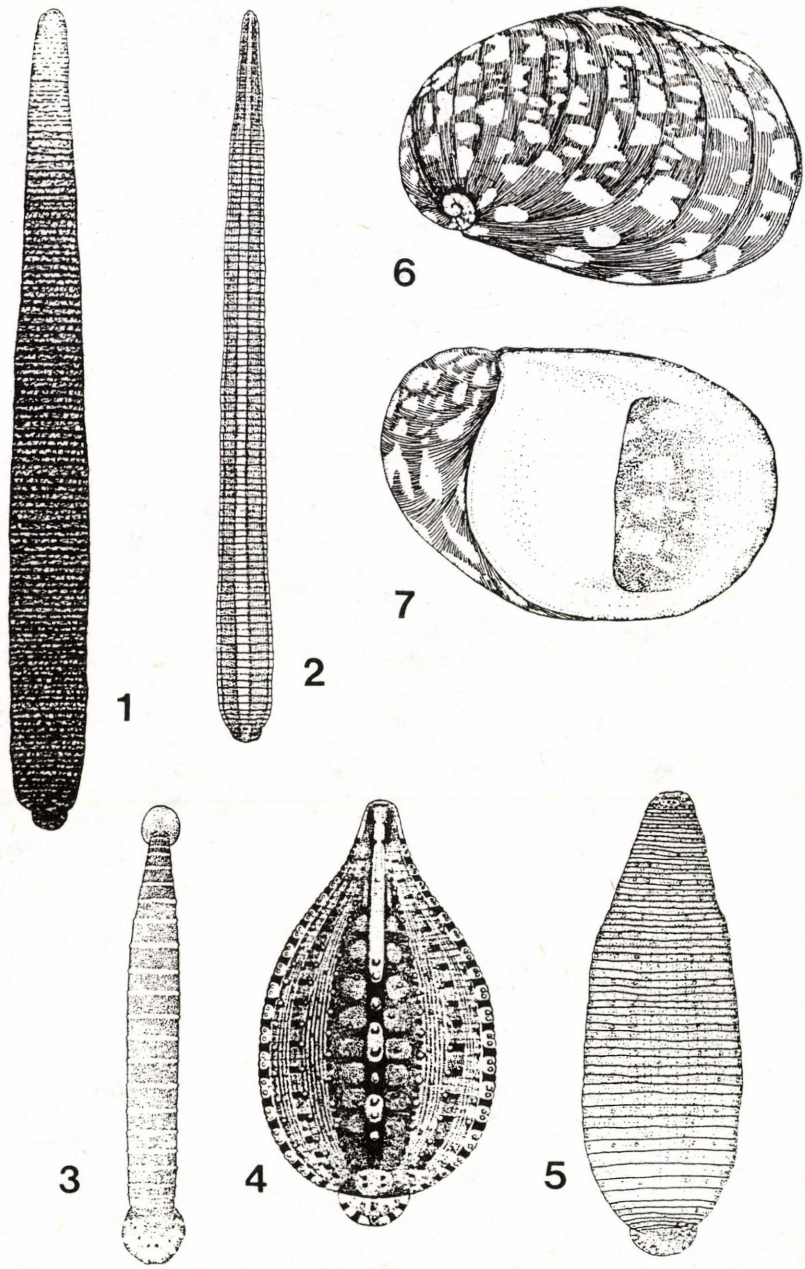


Fig. 1. *Dina apathyi*, Soroksári Duna at Dunaharaszti, Hungary
Fig. 2. *Dina lineata*, Weidenbach at Weikendorf, Austria
Fig. 3. *Piscicola haranti*, Rábca at Győr, Hungary
Fig. 4. *Placobdella costata* (from DRESSCHER & ENGEL 1960), Netherlands
Fig. 5. *Batracobdella algira*, Danube (Prater) near Vienna, Austria
Figs 6-7. *Theodoxus fluviatilis*, Danube at Érd-Ófalu, Hungary

ches on floating aquatic plants (Danube, March), sometimes in swampy dead-water pools (Leitha), in bulrush areas and flood plains (Zala) near the main stream. Elsewhere the species is a remarkable member of the Potamon biocoenosis in lowland rivers with warm water in summers. A lot of records are known from the plain of the upper Rhine (Germany, France) and the Hungarian Great Plain (Austria, Hungary). *G. concolor* was found frequently in the lower reaches of the rivers Danube, March, Leitha and Zala. Its distribution is not only restricted to this part of the Danube Basin. Several isolated populations exist in tributaries along the upper Danube, especially in effluents of large exorheic lakes.

Batracobdella algira (Moquin-Tandon, 1846) (Fig. 5)

Localities: Danube near Vienna (A), in a temporary pond in the Prater-area (dead-water reaches of the Danube), 12. Nov. 1989, May 1990.

The species was found for the first time in Central Europe and is one of the present members of the Ponto-Mediterranean fauna. As far as the published information goes, *B. algira* has a wide range of distribution in the Mediterranean countries including Northern Africa. The leech was found also in the southern parts of the European Soviet Union (LUKIN 1976). Populations are known from different kinds of standing and slowly flowing water bodies. In the northern parts of the settled area, the species seems to be restricted to flood plains of large rivers. Its alleged occurrence may be possible in the Yugoslavian reach of the Danube (SKET 1968). Another occurrence of *Batracobdella paludosa*'s (EPURE 1947), might be that of *B. algira*, considering the author's description. Until now, it is not possible to confirm the complete range.

Placobdella costata (Fr. Müller, 1846) (Fig. 4)

Localities: Danube in Baranja (YU) see MIKUSKA & GEC (1970); Balaton-area (H), Kiskunság (H) see SOÓS (1963); Bátorliget (H), in a pond, 28. Sept. 1990, leg. FORRÓ & NESEMANN (near to a tributary of the River Tisza).

The species is a temporary ectoparasite on the fresh-water turtle (*Emys orbicularis*) and on other vertebrates. Its range of distribution has centres in the Ponto-Mediterranean and Baltic area, but *P. costata* occurs sporadically elsewhere in Central- and Western Europe. This is one of the most common leech species in the eastern Mediterranean area (RÜCKERT 1985). Also it is known from several localities in the Hungarian Great Plain (SOÓS 1963, MIKUSKA & GEC 1970), the northern lowlands of Central Europe (DRESSCHER & ENGEL 1960, AGAPOW 1975, HECHT 1930) and from the British Isles (ELLIOTT, MUGRIDGE & STALLYBRASS 1979). Further alleged records, listed in limnological papers, seem to belong to *Hemiclepsis marginata* (O.F. Müller, 1774). This leech found frequently in large rivers too is often confused with *P. costata* (Autrum, 1958). Actually the present material gives a picture of the disjunct range in Central Europe. In the Danube Basin *P. costata* is naturally restricted to the plains. We have no certain proof about its original existence in the upper Danubian reach.

Fam. Piscicolidae

Piscicola haranti Jarry, 1960 (Fig. 3)

Locality: Rábca near Győr (H), near the confluence of the Rábca and the Mosoni Duna, 19. Jan. 1991, leg. MÖSSMER & NESEMANN.

The fish leeches have developed several endemic taxa in the drainage area of the Ponto-Caspian Sea. *P. haranti* is new to the Hungarian fauna and the Danube

Basin. The species was known only from the type locality near Montpellier in France. It was never recognized in Central European rivers. Therefore we can assume a new working hypothesis of a wide Ponto-Mediterranean range. A short description of the outer morphology for the Rábca-material is given in NESEMANN (1991c).

Fam. Erpobdellidae

Erpobdella nigricollis (Brandes, 1900) (Fig. 10)

Localities: Danube near Ásványráró (H), Dunaág, Felsősziget, km 1817. 23. Oct. 1990; Danube at Gönyü (H), km 1791.4, 23. Oct. 1990; Soroksári Duna at Dunaharaszti (H), 20. Jan. 1989, leg. FORRÓ & NESEMANN; Ráckevei Duna at Szigethalom (H), 8. Jan. 1991, leg. FORRÓ & NESEMANN; Mosoni Duna between Bócsa and Vének (H), 23. Oct. 1990; Leitha (Lajta) upstream Nickelsdorf (A), 26. Oct. 1990; Zala SE Fenékpuszta (H), 20. Jun. 1990, leg. FORRÓ & NESEMANN; Zala in the Kis-Balaton reach (H), 21. Jun. 1990, leg. NESEMANN; Rába at Győr (H), 28. Jul. 1990; Rába near Rábapatona (H), 28. Jul. 1990; Rába near Szany (H), Aug. 1990; Rába near Vág (H), Aug. 1990; Rábca near Győr (H), 19. Jan. 1991, leg. MÖSSMER & NESEMANN; March (Morava), from ten localities in the main stream between Markthof and Hohenau (A), Apr.-Aug. 1990; Thaya near Hohenau (A), Aug. 1990; Thaya near Rabensburg (A, CS), Aug. 1990; Thaya near Bernhartsthal (A, CS), 27. Oct. 1990. For further records (H) see SOÓS (1963, 1967).

E. nigricollis is distributed in Central and Eastern Europe. The species was found from the southern parts of Finland (KOLI 1961) to Syria (RÜCKERT 1985). Hitherto its occurrence has not been ascertained for the British Isles, the Iberian and Italian Peninsula and for Greece. *E. nigricollis* belongs to the Potamon (Eulimnion-) biocoenosis without exception. It is one of the most important leech species in large rivers and occurs very frequently in slowly flowing reaches. In the Danube Basin *E. nigricollis* has a disjunct range, the species has not occurred upstream the Moson reach and it is completely lacking from Austria. A separated colonization was detected in the Bavarian reach between Regensburg and Passau. This fact is understandable as a postglacial relict (Atlanticum) of its former distribution. Several aquatic animals show the same distribution pattern in the Danube Basin.

Erpobdella testacea (Savigny, 1822) (Fig. 11)

Localities: Zala SE Fenékpuszta (H), 20. Jun. 1990, leg. FORRÓ & NESEMANN; Zala in the Kis-Balaton reach (H), 21. Jun. 1990, leg. NESEMANN; March (Morava) near Schlosshof (A) in a dead-water reach, from three samples, 21. Feb., 22. and 23. Apr. 1990; March (Morava) near Sierndorf (A) in a secondary branch, 20. May 1990; Loimersdorfer Graben E Engelhartstetten (A), a small tributary of the River Russbach W Devin, Oct. 1990. For further records (YU) see MIKUSKA & GEC (1970).

The species has a distribution pattern similar to that of *E. nigricollis*. In contrast it prefers swampy running waters with a slow velocity of flow. It is often very abundant in the shallow littoral zone of lakes. Its disjunct range of distribution includes the western Palaearctis. In some parts of the Mediterranean drainage area, *E. testacea* can be common locally in Potamon and Eulimnion biocoenoses of lowland rivers and lakes (CHIAUDANI & MARCHETTI 1984, JOHANSSON

1927, SAPKAREV 1970). There it is a substitute for *E. nigricollis*. The leech *E. testacea* is very rare in the hilly and mountainous areas of Central Europe, where its range is restricted. The species has not been found anywhere in the upper reach of the River Danube yet. The northwestern distribution in this river basin was confirmed in Austria. The flood plain of the lower River March represents the border of the settled area.

Dina punctata Johansson, 1927 (Fig. 8)

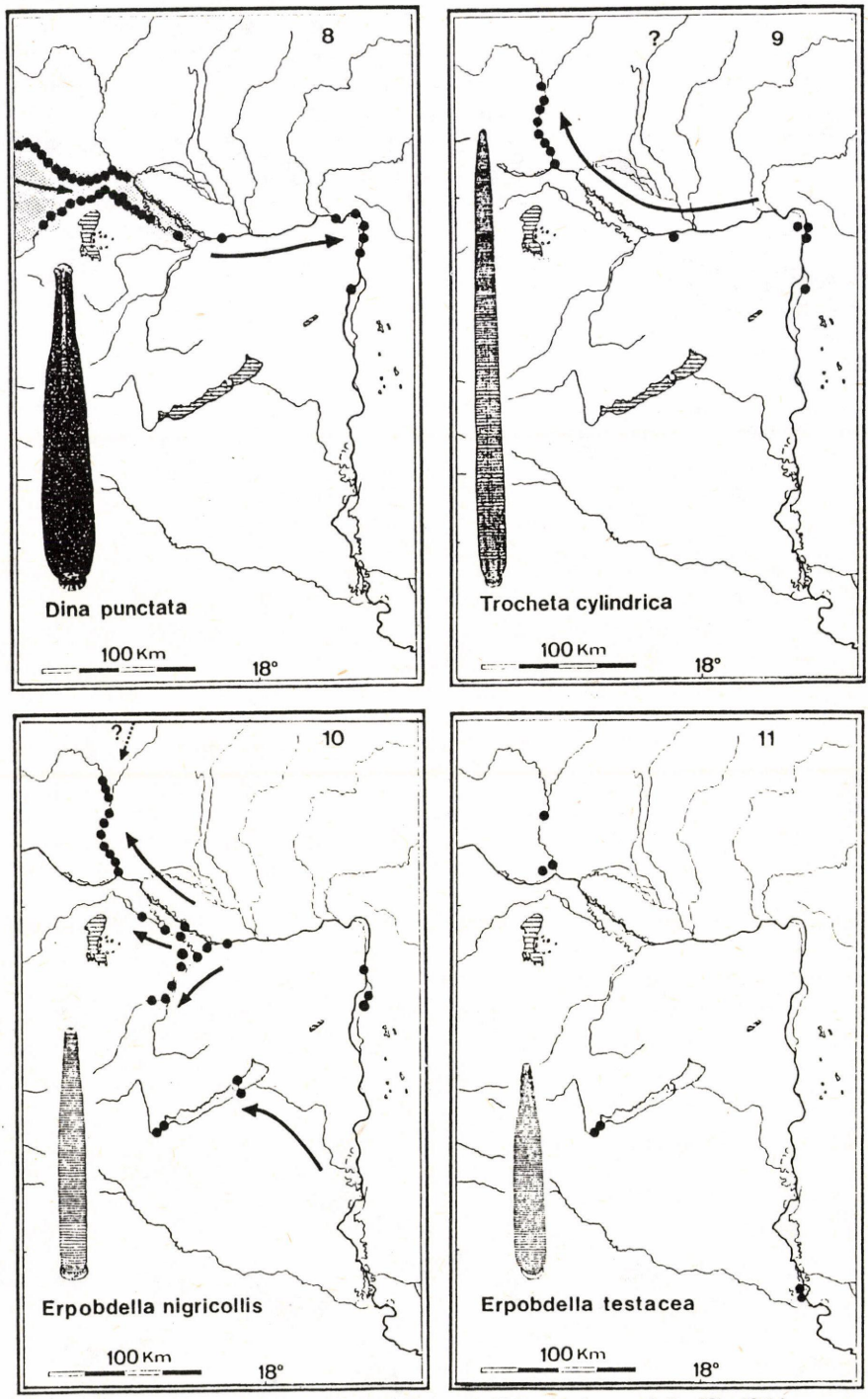
Localities: Danube at Érd-Ófalu (H), km 1625.4, 30. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Budapest, Szabadság-híd (H), km 1645.3, 15. Oct. 1988; Danube at Szob (H), km 1706.6, Oct. 1989, leg. PUKY & NESEMANN; Danube at Vác (H), km 1680.4, Oct. 1989, leg. PUKY & NESEMANN; Danube at Nagymaros (H), km 1694.7, Oct. 1989, leg. PUKY & NESEMANN; Danube near Gönyü (H), km 1791.4, 23. Oct. 1990; Mosoni Duna at Dunaszeg (H), 23. Oct. 1990; very common in the Danube (A) between Wolfsthal (km 1876) and Stockerau (km 1950), see NESEMANN (1989a); March (Morava) near Markthof (A), 24. Mar. 1990; Lajta at Mosonmagyaróvár (H), 3. Apr. 1990; Leitha at Nickelsdorf (A), 26. Oct. 1990; Leitha at Hollern (A), 26. Oct. 1990; Leitha near Pachfurth (A), 27. May 1990; Leitha at Bruck (A), 3. Jun. 1990; very common in the middle reach of the River Leitha (A) between Bruck and Ebenfurth (1988-1990).

The closely separated species seems to belong to a monophyletic group of the subfamily Trochetinae, including *D. apathyi, D. stschegolewi* (LUKIN & EPSHTEIN 1960) and several undiscussed forms. *D. punctata* is widely distributed in the Ebro-, Rhine-, Po- and upper Danube Basins. It originated from the western Paleoeuropean or Euromediterranean fauna (KINZELBACH 1987), unlike *D. apathyi* and *D. stschegolewi*, which originated from the eastern (Pontosarmatian) fauna. *D. punctata* is a characteristic member of the biocoenosis in fast flowing mountain streams and circum-alpine rivers with a strong bed load transport of round stones. The groundtype of distribution pattern is similar to that of rheophilic Cyprinid fish *Leuciscus souffia* (Risso, 1826). *D. punctata* is mainly located at altitudes higher than 300 meters above sea level. The species is the most abundant leech in the upper Danubian Basin in Germany and Austria. It becomes rare in the Hungarian Danube around Budapest. Its occurrence spreads downstream to Érd. Here *D. punctata* lives sporadically at undercut slopes on gravely and stony bottoms. In the following stretches *D. lineata* gradually becomes dominant compared to the other species listed (Szalkszentmárton, Dunaföldvár). In general *Trocheta cylindrica* (March, Thaya), *Dina punctata* and *D. lineata* (Danube, Lajta) occur mainly allopatrically.

Dina apathyi Gedroyc, 1916 (Fig. 1)

Localities: Ráckevei (Soroksári) Duna near Dunaharaszti (H), 20. Jan. 1989, leg. FORRÓ & NESEMANN, 9. Oct. 1989, leg. PUKY & NESEMANN.

It is a Ponto-Caspian species which is rarely found, but widely spread in the drainage area of the Black Sea and Caspian Sea. A general description, based on the Hungarian records, was previously given (NESEMANN 1991b). This semi-aquatic species inhabits lowland rivers and lakes. It prefers stagnant water bodies of secondary branches, wherein it has already been reported by MIKUSKA & GEC (1970).



Figs 8-11. Distribution of some Erpobdellidae in rivers of the Kisalföld

Dina lineata (O.F. Müller, 1774) (Fig. 2)

Localities: Danube at Dunaföldvár (H), km 1560.8, 31. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Szalkszentmárton (H), km 15775.31. Jan. 1991, leg. WIMMER & NESEMANN; Danube near Mühleiten (A), in a dead-water reach "Kühwörther Wasser", Feb. 1989; Danube near Vienna (A), in a dead-water reach "Lusthauswasser", Jun. 1989; Danube-Krumpenwasser, a secondary branch near Stockerau (A), 19. Mar. 1989; March (Morava) near Schlosshof, in a dead-water reach (A), 22. Apr. 1990; Leitha at Pachfurth (A), in a dead-water reach, 2. Jun. 1990, leg. MANN & NESEMANN.

The species is widely distributed in the western Palearctic except for the northern parts of Scandinavia. Several easily distinguishable subspecies have been described from Mediterranean countries. All forms detected in the Hungarian Great Plain belong to the nominated subspecies. This leech appears in swampy dead waters of lowland rivers and streams and is occasionally abundant in reed ponds and in the habitats of *Salix alba*. It becomes more or less common in the main stream of the River Danube downstream Budapest. Hitherto the species has not been reported from upper Danube reaches. Its occurrence in Austria is restricted to dead-water reaches in the east of Vienna.

Trocheta cylindrica Örley, 1886 (Fig. 9)

Localities: Danube near Alsógöd (H), km 1668.8, 6. Mar. 1989, leg. FORRÓ & NESEMANN; Danube near Vác (H), km 1690.4, 6. Nov. 1989, leg. PUKY & NESEMANN; Soroksári Duna near Dunaharaszti (H), 8. Nov. 1989, leg. PUKY & NESEMANN; Szentendre Duna near Szentendre (H), 31. May 1989, leg. PUKY & NESEMANN; Danube and Cuhai-Bakony-ér (H) downstream Gönyü (H), km 1789.8, 3. Apr. 1990; March (Morava) between Markthof and Sierndorf (A), from six samples, Apr.- Aug. 1990; Thaya (Dyje) near Hohenau (A, CS), Aug. 1990.

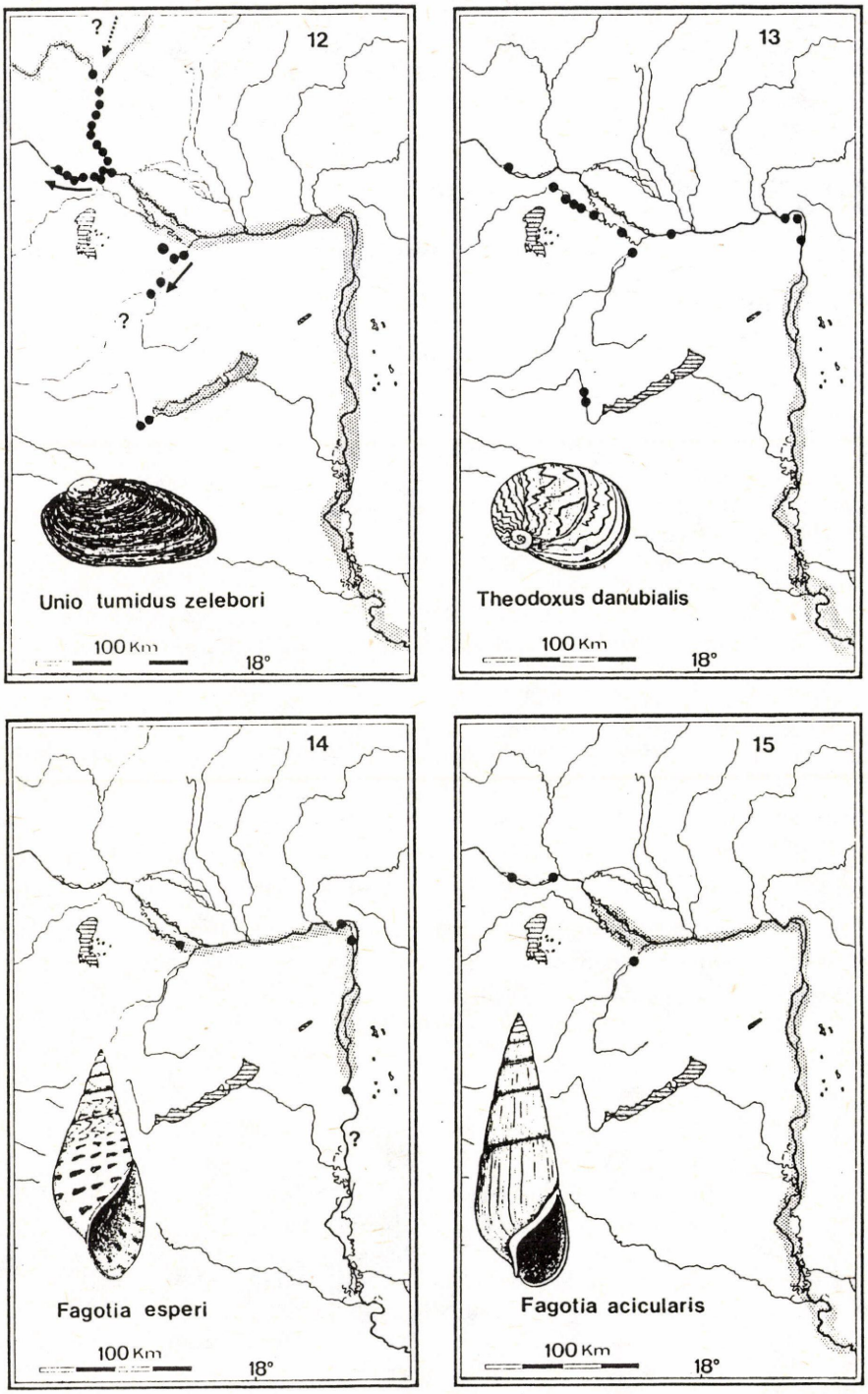
This semiaquatic (amphibious) species is quite separated from *Trocheta bykowskii* Gedroyc, 1913 regarding its habitat preferences, ecology, geographical distribution and morphology. It is a typical member of the eastern Paleoeuropean fauna. The distribution area is extended from the southern Soviet Union (Georgia, under the name *Trocheta subviridis danastrica* Stschegolew, 1938) to Greece and from Anatolia into the Pontosarmatian Basin. The range is bordered in the March-Thaya basin, wherein it is a substitute for *Dina punctata*. The species belongs to the Potamon biocoenosis and prefers muddy river banks. Throughout the investigated area it is restricted to large lowland rivers.

Gastropoda

Fam. Neritidae

Theodoxus danubialis (C. Pfeiffer, 1828) (Fig. 13)

Localities: Danube downstream Gönyü (H), km 1783.1, 3. Mar. 1990; Szentendre Duna near Szentendre (H), 31. May 1989, leg. PUKY & NESEMANN; Szentendre Duna between Leányfalu and Tahitótfalu (H), 31. May 1989, leg. PUKY & NESEMANN; Szentendre Duna at Dunabogdány (H), 31. May 1989, leg. PUKY & NESEMANN; Danube at Visegrád (H), km 1693.6, leg. PUKY & NESEMANN; Mosoni Duna at Dunaszeg (H), 23. Oct. 1990; Danube-"Kühwörther



Figs 12-15. Distribution of some Danubian freshwater mollusca in rivers of the Kisalföld

Wasser" (a dead-water reach) near Schönau (A), downstream Vienna, Oct. 1990; Rába at Győr (H), 28. Jul. 1990; Zala at Bókaháza (H), 31. May 1990, leg. FORRÓ & NESEMANN; Zala at Zalavár (H), 31. May 1990, leg. FORRÓ & NESEMANN; Lajta at Mosonmagyaróvár (H), 3. Mar. 1990; Leitha-Komitatskanal (Lajta bal parti csatorna) near Nickelsdorf (A), Sept. 1987; Leitha at Nickelsdorf (A), Sept. 1987, Oct. 1990; Leitha at Zurndorf (A), Sept. 1987; Leitha downstream Hollern (A), 26. Oct. 1990; empty shells of freshly dead animals also were collected from the Hungarian reaches of the Danube at km 1625 and 1560.

This species originally has a Sarmatian distribution and is a typical member of the Danubian fauna. It also colonized some adjacent drainage areas (Po, Axios) during the Pleistocene, where it still lives as a relict. *T. danubialis* is the most common Neritidae of the Carpathian Basin. Recently it has settled in the Danube upstream to Bavaria near Kehlheim (LEUCHS & TITTIZER 1989). It seems to have a partially disjunct range, because it prefers mostly lowland rivers with a moderate velocity of flow. It was found in large numbers in the Danube only in the Hungarian reaches. Its recent occurrence in the Austrian Danube is restricted to abandoned river lakes with a fauna very rich in Ponto-Caspian species. Elsewhere *T. danubialis* colonizes the lower reaches of other rivers (Lajta, Rába, Zala) at high densities of individuals.

Theodoxus fluviatilis (Linnaeus, 1758) (Figs 6-7)

Localities: Danube at Érd-Ófalu (H), km 1625.4, 30. Jan. 1991, leg. WIMMER & NESEMANN, for further records (Tisza) see PINTÉR, RICHNOVSZKY & SZIGETHY (1979).

T. fluviatilis is a new prosobranchiate snail to the Hungarian Danube. It is widely spread all over Europe including Anatolia, but does not belong to the original Danubian fauna. Its occurrence in the Carpathian Basin was first recognized for the river Tisza (HORVÁTH 1943), wherein *T. fluviatilis* allopatrically takes the place of *T. danubialis*. In general the working hypothesis is accepted, that *T. fluviatilis* is a Pleistocene immigrant. The species could possibly enter the upper Tisza by river capture, arriving from the Baltic drainage area.

The species is a characteristic member of the rheophile fauna of large rivers and littoral zones of lakes. In the southern parts of the settled area, *T. fluviatilis* is also known from springs and brooks occasionally. Its geographical distribution pattern in the Rhine Basin is very similar to that of the leech *Erpobdella nigricollis* and the freshwater bivalve *Unio tumidus* Philipsson, 1788. It prefers overflowed gravelly and stony bottoms.

Fam. Thiaridae

Fagotia acicularis (A. Ferussac, 1823) (Fig. 15)

Localities: Danube at Dunaföldvár (H), km 1560.8, 31. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Érd-Ófalu (H), km 1625.4, 30. Jan. 1990, leg. WIMMER & NESEMANN; Szentendre Duna between Tahitótfalu and Leányfalu (H), 31. May 1989, leg. PUKY & NESEMANN; Danube at Visegrád (H), km 1693.6, 31. May 1989, leg. PUKY & NESEMANN; Danube near Hainburg (A), in a secondary branch "Unterer Tiergartenarm", Apr. 1989; Danube near Schönau (A), in a dead-water reach "Kühwörther Wasser", Oct. 1990; Rába at Győr (H), 28. Jul. 1990.

The members of the Thiaridae family originally belong to the Pontosarmati-

an Basin, the range of distribution includes mainly the Danube. *F. acicularis* occurs in the Danube and is common in thermal springs of this river basin too, wherein it lives together with the Pliocene relict *Theodoxus prevostianus* (C. Pfeiffer, 1828). These populations are completely separated from those in large rivers. In general *F. acicularis* inhabits slowly flowing reaches of the Danube and large tributaries (Rába). It is present in high abundances in secondary branches downstream Vienna, but its occurrence in the main stream starts at first downstream Gönyü (BOTHÁR 1966). This species is less common than *F. esperi* in the whole Hungarian reach.

Fagotia esperi (A. Ferussac, 1823) (Fig. 14)

Localities: Danube at Dunaföldvár (H), km 1560.8, 31. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Érd-Ófalu (H), km 1625.4, 30. Jan. 1991, leg. WIMMER & NESEMANN; Danube at Visegrád (H), km 1693.6, 31. May 1989, leg. PUKY & NESEMANN; Szentendre Duna at Szentendre (H), 31. May 1989, leg. PUKY & NESEMANN; Szentendre Duna between Tahitótfalu and Leányfalu (H), 31. May 1989, leg. PUKY & NESEMANN; Mosoni Duna at Dunaszeg (H), 23. Oct. 1990.

The second member of the Thiaridae is the most frequent prosobranchiate snail together with *Lithoglyphus naticoides* (C. Pfeiffer, 1828) (BOTHÁR 1966). *F. esperi* is a characteristic member of the Danubian Potamon biocoenosis. Its distribution is extended upstream towards the Mosoni Duna, but no records are known from the Austrian reaches or the large tributaries. The Holocene evidence is known from the lower reach of the River Lajta. The species, rarely found in earlier times, becomes a common member of the Danubian fauna during the last 25 years.

CONCLUSIONS

Zoogeographical barriers and pathways

We can distinguish between several groups of the Potamon biocoenosis, which had been able to inhabit the upper courses of the rivers, originally starting from the lower or middle reach of the river Danube since the end of pleistocen glaciation. According to SOÓS (1934) the invetigated rivers are divided in districts or zones as shown on Fig. 19. The most important barriers or pathways are the narrow valleys, where the Danube breaks through the mountains. The reaches are often characterised by riffles, rocky slopes with a strong velocity of flow and high gradient and the absence of deadwaters and floodplains (see Fig. 18). The narrow valleys are unfordable barriers for many non-rheophile aquatic organisms. The whole course of the river Danube is divided into isolated basins and plains (SOÓS 1934). For zoogeographical history the most important plains (Fig. 18) along the upper and middle reach exist in Bavaria between Regensburg and Vilshofen (Gauböden), in Austria between Vienna and Hainburg (Wiener Becken, Kisalföld) and in Hungary (Kisalföld, Alföld).

A large number of species seems to be restricted to the central Hungarian Great Plain (Alföld, zone 1 on Fig. 19). Their distribution is bordered at the middle reaches of the rivers Tisza and Danube (downstream the Dunakanyar). Some examples presented in this paper are *Dina apathyi, Theodoxus fluviatilis,* perhaps *Placobdella costata,* but also the amphipods *Obesogammarus obesus* and *Orchestia cavimana*. The "Wiener Pforte", upstream towards zone 5 is a barrier for

Glossiphonia paludosa, Batracobdella algira, Fagotia acicularis, Viviparus acerosus and *Unio tumidus zelebori* (see also Fig. 12). The distribution patterns recently found for the crustaceans *Limnomysis benedeni, Dikerogammarus villosus* and *Chaetogammarus ischnus* are very similar (NESEMANN, unpublished). The "Hainburger Pforte" or "Porta Hungarica" (point of intersection, zone 2, 3 and 4) separates many lowland rivers from the upper Danubian river basin. The following species do not occur in the Austrian Danube even today: *Erpobdella testacea, E. nigricollis, Trocheta cylindrica, Valvata (Borysthenia) naticina* and *Fagotia esperi.* Its range of extension is bordered at the Kisalföld area (Szigetköz), while the three leech species had been able to enter the plain of the lower river March (Morava, zone 3) into northwestern direction.

The influence of tributaries of the Danubian fauna

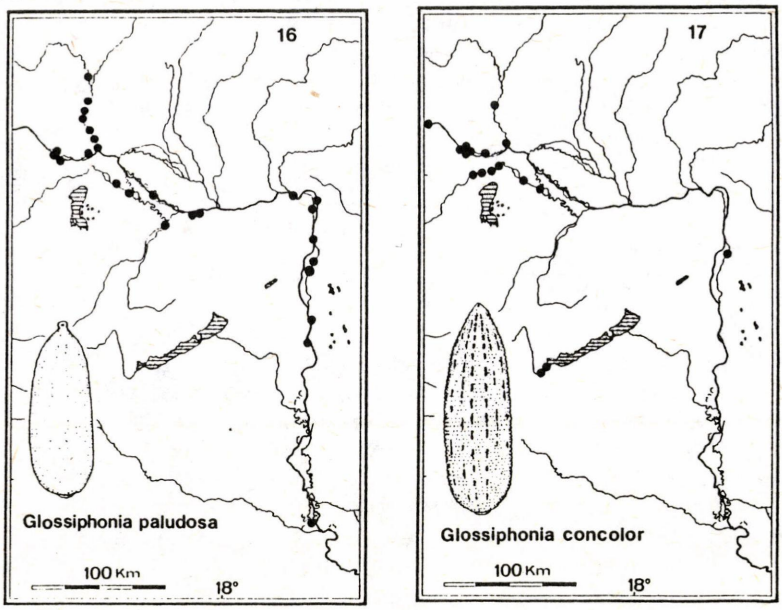
Another important fact for the biological zonation is the confluence of large tributaries, which are able to influence the regimen of the River Danube. The Hungarian distribution of several leeches and snails is recently bordered upstream at the confluence of the lowland river March. Isolated populations (*Erpobdella nigricollis, Viviparus acerosus, Valvata (Borysthenia) naticina*) of the Bavarian Danube, more than 300 km away from the Hungarian Great Plain, are restricted to the lowland-river-like reach upstream from Passau. They are considered postglacial relicts of its former spreading during warm periods (Atlanticum).

The Austrian Danube is strongly influenced by the river Inn and other tributaries of the alpine mountains. The main stream between Passau and Vienna is more or less homogeniously populated with the typical biocoenosis of the upper Danube, including only the frequent leech species *Dina punctata, Glossiphonia complanata* and *Erpobdella octoculata.* The radical change of the biocoenosis downstream Vienna is not only caused by the abiotic characteristics. It is also understandable as a summarised result of the confluence of many typical lowland rivers between Bratislava and Szob (zone 2 on Fig. 19).

Biological characteristics and river zonation

Some interesting similarities are found between the faunal composition of the main stream of the Danube, the anabranches and dead-water reaches. The communities of several deadwaters near Vienna resemble the Hungarian main stream with high abundances of *Glossiphonia paludosa, Dina lineata, Fagotia acicularis, Theodoxus danubialis, Viviparus acerosus, Lithoglyphus naticoides, Sphaerium rivicola* ssp. and *Unio tumidus zelebori.* The listed species are common in the middle reaches. The uppermost localities are recorded from lakes and deadwaters of the alluvial floodplain, while its occurrence in the main stream is bordered at the Moson reach. Therefore the importance of "lakes" and secondary branches is easily understandable, which simulate environmental characteristics of high-order-streams (zone 1) (OTTO & BRAUKMANN 1983) along the upper and middle reaches (zone 4) of the river. Large anabranches with the possibility of faunal exchange contain the highest diversity of leech species (MIKUSKA & GEC 1970). Some interesting examples along the investigated reach of the Danube are to be shown: the Kühwörther Wasser between Mühleiten and Schönau, the Mosoni Duna and the Ráckevei Duna.

In general most of the discussed leeches and molluscs, except *Dina punctata*, are typical members of the Danubian Potamon biocoenosis. They are restricted to the rivers of the Hungarian reaches or occur only in relict populations along the



Figs 16-17. Distribution of some Glossiphoniidae in rivers of the Kisalföld

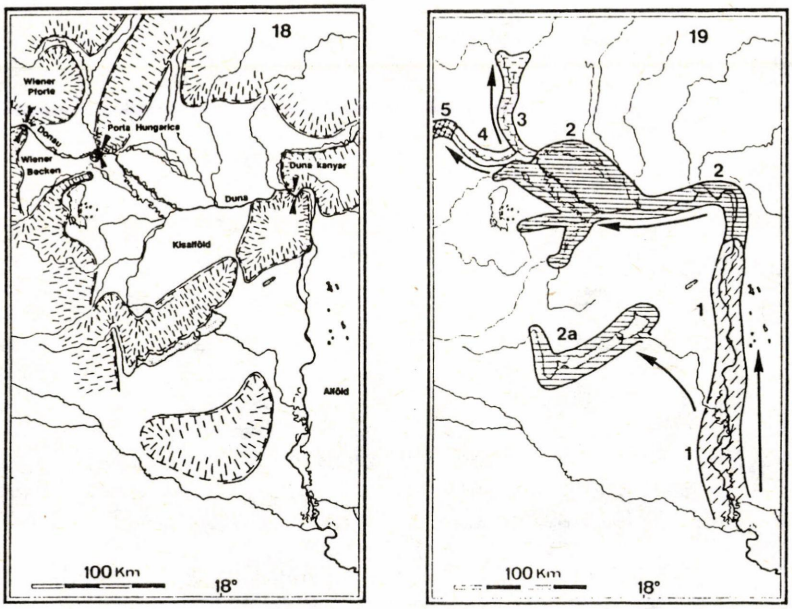


Fig. 18. The most important plains, barriers (mountains) and pathways (narrow valleys) for aquatic organisms along the middle reach of the river Danube
Fig. 19. Zoogeographical division of the Potamon biocoenosis, according to SOÓS (1934) (For explanation of the numbers see text)

upper Danube in Austria and Germany. In contrast to this group, *Dina punctata* is a member of the old fauna of the upper Danubian river basin, which was formed during Pleistocene. Also the fish *Leuciscus souffia* and the freshwater mussel *Unio crassus cytherea* belong to that fauna, which is well adapted to the habitats of the Rhitron.

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